Age and geographic variation in the Bearded Vulture *Gypaetus barbatus* (Linnaeus, 1758)

by

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Introduction

From an evolutionary point of view two kinds of biological variation can be distinguished. The first, called geographic variation, occurs when there are differences among spatially segregated populations of a species. The second, called individual variation, concerns differences among individuals of a single population, which can be the consequence of sex, age, season, genetic polymorphism or other factors. This paper deals with plumage changes with age and geographic variation in the Bearded Vulture (*Gypaetus barbatus*).

Juvenile Bearded Vultures have a uniformly dark plumage, whereas in adults dark colors are particularly contrasted with white parts. Adult plumage is acquired at about five to six years of age (see Heinroth & Heinroth, 1967, Boswall, 1970 and others). Our purpose is to study: a) the process of plumage variation from juveniles to adults and b) the correspondence among intermediate plumages and age. Both subjects are not sufficiently well-know at present (Glutz et al., 1971).

On the other hand, numerous authors have drawn attention to the variations in size and pattern among Bearded Vultures from different geographic areas, distinguishing between up to 4 or 5 subspecies (Hartert, 1912—1921, Swan, 1945, Vaurie, 1965, Dementiev & Gladkov, 1966, Brown & Amadon, 1968, Glutz et al., 1971.) However, the usual taxonomic approach to the subject implies that the study of geographic variation is set within the framework of the subspecies concept, which makes an unibased analysis of variation difficult (Selander, 1971). In this paper morphological characters of *Gypaetus barbatus* which vary geographically are analysed without a priori regard for subspecies.

Material and methods

Analysis has been limited to the biometric and plumage variations of 252 study skins preserved in museum collections and representing the whole range of the species. Specimens were examined from the following collections: British Museum (Natural History),

Tring: 73; Museum für Naturkunde der Humboldt-Universität, Berlin: 48; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn: 47; Rijksmuseum van Natuurlijke Histoire, Leiden: 16; Zoologische Sammlung des Bayerischen Staates, München: 15; Natur-Museum Senckenberg, Frankfurt am Main: 13; Muséum d'Histoire Naturelle de Nantes, Nantes: 11; Naturhistorisches Museum, Bern: 8; Staatliches Museum für Naturkunde, Stuttgart: 8; Muséum d'Histoire Naturelle, Genève: 6; Muséum National d'Histoire Naturelle, Paris: 2; Muséum d'Histoire Naturelle de Nîmes, Nîmes: 2; Station Biologique de la Tour du Valat, Le Sambuc: 1; Zoölogisch Museum der Universiteit van Amsterdam: 1; Estación Biológica de Doñana, Sevilla: 1. The conservation state of the different skins was quite variable and we were not able to examine all the characters in every specimen.

After having examined the first 100 specimens we selected 16 two-state characters and two multistate characters in which variation with age could be identified. All the specimens analysed were grouped according to these characters into 19 homogeneous types (Table 1). In each case, the presence of the character was noted as "1" and the lack of it noted as "0". Similarity among types was calculated with the Gower coefficient, Sg (Sneath & Sokal, 1973). Thus, we obtained a similarity matrix among different types (Table 2) which has been examined with the multivariate classification analysis U.P.G.M.A. (Sneath & Sokal, 1973) to obtain the corresponding dendrogram. We indicate below the two-state presence—absence characters selected, preceded by a number. They shall henceforth be referred to by that number.

Head region:
1.— Brown-blackish feathers in the crown (Fig. 1: 1).
2.— Brown semiplumes in the crown (Fig. 1: 2).
3.— White semiplumes with a variable proportion of black bristles in the crown (Fig. 1: 3 and 4).
4.— Brown-blackish feathers in the occiput and the nape (Fig. 1: 1, 2 and 3).
5.— White feathers in the occiput and the nape (Fig. 1: 3 and 4).
6.— Black, long bristles on the upper mandible, joining the bristles of the lower mandible (if the bristles were brown and did not join the ones of the lower mandible, the character was considered absent).

Ventral region:
7.— Brown feathers in the breast and ventral region, excluding the feathers defined as "pectoral band" in the geographic variation study.
8.— White feathers in the same region.

Dorsal region between the wings:
9.— Wide, brown feathers with a white tip (Fig. 2: 4).
10.— Wide brown feathers (Fig. 2: 5).
11.— Long, thin feathers, brown, blackish or pied with different colors. All of them are different from those which typically appear in adults and correspond to the following character (Fig. 2: 6 and 7).
12.— Long, thin feathers, with a dark border, steel-gray center and white rachis and apex (Fig. 2: 8).

Wing:
13.— Uniform brown marginal coverts (Fig. 2: 1).
14.— Two-colored marginal coverts irregulary distributed (Fig. 2: 2).
15.— Small marginal coverts as in character 12 (Fig. 2: 3).
16.— Sharp second primary (when the border of the second primary is somewhat rounded, this character was considered lacking; Fig. 2: 9 and 10).
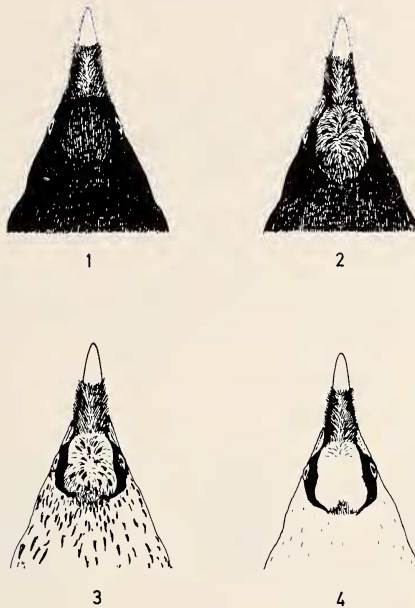
Fig. 1: Different patterns of plumage in the head region. 1: Only brown-blackish feathers are present in the crown, the occiput and the nape. The "eyebrow" is not differentiated. 2: It differs from 1 by the presence of brown semiplumes in the crown and an incomplete dark-brown "eyebrow". 3: Brown semiplumes and white semiplumes in the crown. Brown-blackish feathers and white feathers in the occiput and the nape. Well differentiated black-coloured "eyebrow". 4: White semiplumes in the crown. White feathers in the occiput and the nape. "Eyebrow" like 3.

Each of the states in the multistate characters was considered to operate as a two-state character, as follows:

Eyebrow: A thin fringe in the superciliary region formed by bristles. We distinguished three states:

17.— Without differentiated eyebrow (Fig. 1: 1).
18.— With an incomplete dark-brown colored eyebrow (Fig. 1: 2).
19.— Complete eyebrow, well differentiated, black colored (Fig. 1: 3 and 4).

Steel gray color in the web of the big scapulars and flight feathers. Three states can be distinguished:

20.— Lack of steel-gray color.
21.— Presence of steel-gray color but never covering more than 50 % of the vane.
22.— Presence of steel-gray color covering most of the vane.

The following measurements were taken of each specimen:

WL = Wing length with tape following the curvature
TL = Tail length from the base of the rectrices

FT = Length of the tarsus
BL = Beak length from the culmen
BC = Beak length from the cere

The tonality and pattern in different body areas was also examined and described.

For the biometric analysis we used data obtained from all the specimens, adults as well and young. We previously compared the average measurements of adults and young from the best represented population of the sample (Ethiopia) without finding significant differences among them, although adults are a little bigger (Student "t" test). Differences among males and females are not significant in wing, tarsus and tail, but females tend to be bigger. Both beak measurements of females are significantly larger than those of males (p < 0.01; Student "t" test) which has led us to do not consider these measurements because the size of the samples is not enough to analyse separately the geographic variation in each sex. Wing length on the other hand is significantly correlated with tail
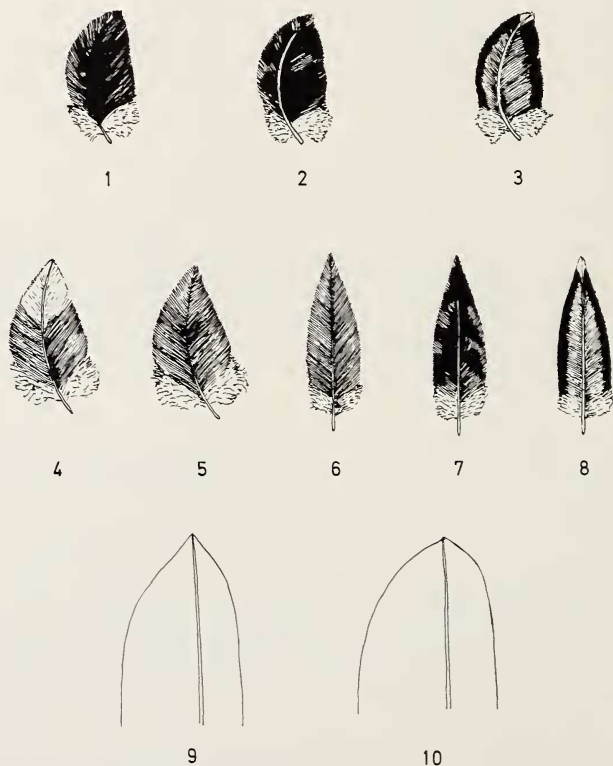

Fig. 2: Different types of feathers used as characters for the analysis of age variation. 1 to 3: small marginal coverts of the wing. 4 to 8: contour feathers of the back. 9 and 10: 2nd primary.

Fig. 3: Populations considered for the study of the geographic variation. Black dots represent localities. CA = Central Asia, IN = India, P = Pakistan, CP = Caucase—Persia, BA = Balkans, AL = Alps, SD = Sardinia, IP = Iberian Peninsula, NA = North Africa, YA = Yemen, ET = Ethiopia, SA = South Africa.

length (r = 0.885; N = 91; p < 0.001) and tarsus length (r = 0.462; n = 91; p < 0.001). We therefore use the wing length as an estimation of the animal's size.

The localities and the considered geographic limits of the populations are shown in Fig. 3. In all cases we have disregarded specimens which came from captivity. For the study of the patterns and color variation only adult specimens (types 14, 13 and 12 in Table 1 and Fig. 4) were considered.

Results

Sequence of plumages

The associations of characters that define the different types of plumages appear in the matrix of data (Table 1). Actually, the types so defined are nothing but phases in which the continuous process (which starts with the plumage of the juvenile that leaves the nest and becomes stable with adult plumage) has been interrupted by the death of the specimen. Therefore, we may assume that the phenetic similarity between types is a good indication of their proximity in the ontogenetic process.

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Table 1: Presence (1) or absence (0) of each one ot the 22 considered characters in the 19 differentiated phenetic types of Bearded Vultures. N: number of specimens of each type.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	N
1	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	33
2	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0	2
3	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	0	0	5
4	1	0	0	1	0	0	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	5
5	1	1	0	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	22
6	1	1	0	1	1	0	1	0	0	1	1	0	1	0	0	0	0	1	0	0	1	0	1
7	1	1	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	1	0	0	1	0	4
8	1	1	0	1	1	0	1	1	0	1	1	0	0	1	0	0	0	1	0	0	1	0	1
9	1	1	0	1	1	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	6
10	0	1	1	1	1	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0	1	1
11	0	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	1	14
12	0	0	1	0	1	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	102
13	0	0	1	0	1	1	0	1	0	0	0	1	0	1	1	0	0	1	0	0	0	1	4
14	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	0	1	0	0	0	1	3
15	0	1	1	1	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1	14
16	0	1	1	1	1	1	0	1	0	0	1	1	0	1	0	0	0	1	0	0	0	1	3
17	0	1	0	1	1	0	1	1	0	1	1	0	1	1	0	0	0	1	0	0	0	1	3
18	0	1	1	1	1	0	1	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1	3
19	0	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	0	1	1

Similarity relations reveal the existence of four well-differentiated groups (Table 2 and Fig. 4). In order to understand the phenogram, it is necessary to consider that juveniles belong to type 1 when they leave the nest (according to various skins from specimens collected in the nest when they had already grown their feathers) and perfect adults belong to type 12. Then, the sequence of appearance of these four groups of plumage in the ontogeny of the Bearded Vulture would be A—B—C—D.

Group A includes type 1, that is juveniles which have not started to molt, and types 2, 3 and 4, which include juveniles which have started the contour molt (generally starting by the back) but still keep the first remiges, sharp and not steel-colored (Table 1). Group B includes specimens different from those of the previous group in that they have at least some of the flight feathers rounded and steel-colored. Besides, brown semiplumes have appeared in their heads and a brown eyebrow is visible. In this group are immatures which have already molted their flight feathers (remiges of the second plumage more rounded than those of the first one are typical in various species of eagles and vultures; Brown & Amadon, 1968, Houston, 1973); they are either finishing their first contour molt or starting the second. Group C includes immatures phenetically closer to adults than to juveniles. They are specimens which either have started the second molt of flight feathers or have already finished it, but are still molting contour feathers.
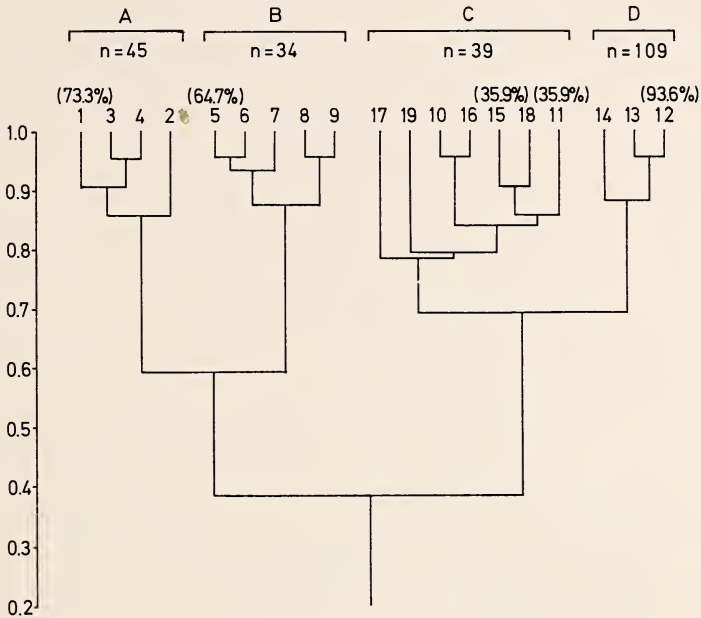
Fig. 4: Similarity dendrogram of the 19 phenetic types of bearded vultures as character-
ized in Table 1. Four guilds (A, B, C, D) are differentiated. N = number of specimens
in each group. ( ) = percentage of individuals corresponding to the best represented type
in each group.

Group D includes specimens with perfect adult plumage (type 12) or with
adult plumage with slight vestiges of immature plumage (types 13 and 14). Type
13 differs from type 12 only in the presence of two-colored marginal coverts,
which may be typical of the first adult plumage. As far as this is concerned, we
must remember that Dementiev & Gladkov (1966) point out the presence of
imperfections in the first adult plumage of Bearded Vultures. Types 13 and 14
probably correspond to specimens in their first adult plumage and type 12 to
adults in subsequent plumages.

The higher frequency of certain types within their corresponding group (Fig.
4) may be due to different facts, namely:

(a) They represent a relative stabilization of the molting process (e.g. types 1 and
12, including juveniles which left the nest and adults).

(b) They comprise periods of time relatively longer than other types of the group
in the molting process (type 5), or

(c) They typify the molting process more frequently followed by the species, as
it seems to be the case of types 11 and 15.

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Table 2: Similarity matrix of the 19 differentiated phenetic types of Bearded Vultures.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	1	.863	.909	.909	.636	.636	.545	.500	.500	.318	.227	.227	.182	.182	.182	.182	.454	.273	.318
2		1	.909	.818	.727	.682	.636	.545	.500	.318	.227	.227	.182	.182	.182	.136	.454	.227	.318
3			1	.954	.682	.636	.591	.500	.545	.318	.227	.227	.182	.182	.182	.136	.454	.227	.318
4				1	.727	.682	.636	.545	.591	.364	.272	.272	.227	.227	.227	.182	.500	.272	.364
5					1	.954	.909	.818	.864	.500	.409	.227	.182	.272	.364	.364	.636	.454	.500
6						1	.954	.864	.909	.545	.454	.273	.227	.318	.409	.409	.682	.500	.545
7							1	.909	.954	.591	.545	.318	.273	.545	.545	.454	.727	.545	.500
8								1	.909	.682	.500	.318	.364	.454	.454	.545	.727	.636	.500
9									1	.636	.545	.273	.318	.409	.500	.500	.682	.591	.545
10										1	.818	.636	.682	.773	.864	.864	.864	.864	.545
11											1	.727	.772	.864	.864	.954	.773	.864	.727
12												1	.954	.864	.773	.773	.773	.682	.818
13													1	.909	.818	.818	.545	.727	.682
14														1	.909	.909	.636	.818	.682
15															1	.909	.773	.909	.773
16																1	.727	.818	.864
17																	1	.818	.773
18																		1	.864
19																			1

Determination of age

It can be assumed that:

(a) *Gypaetus barbatus* starts the molt of its first plumage approximately at the age of 12 months (Hiraldo et al., 1979).

(b) The first adult plumage appears between the age of 5 and 6 years.

(c) Molt of contour feathers last approximately 2 years and remiges a year (Menzbier in Houston, 1973).

(d) Contour molt starts before and finishes after that of the remiges, as we have seen above.

(e) We know also that a captive specimen which died at the age of three years belonged to type 5 and it was about to finish the first molt of flight feathers.

With this information it is possible to assign an approximate age to different types and/or groups in Fig. 4, as it is shown in Table 3.

Table 3: Approximate correspondence among absolute ages and plumage phases in the Bearded Vulture. See text for a description of phenetic types and groups.

Phenetic types	Guild	Aproximate age (months)
1	A	3—12
3,4,2	A	12—21
5	B	21—36
6,7,8,9	B	36—43
10,11,15,16,17,18,19	C	43—60
13,14	D	60—84
12	D	84

Geographical variation in wing length

The distribution of wing measurements in each population and other data of the specimens are given in Fig. 5. The data from Pakistan ($\bar{x}$ = 833.0) have not been shown because of the small sample size (N = 2).

The largest individuals live in central Asia, the size gradually diminishing towards the south and west until the lowest values are reached in Ethiopia, ascending slightly in South Africa. The average wing length in central Asia differs significantly from all the others. In the remaining cases there is always one or more intermediate population which does not differ statistically from any other populations which are compared (Table 4).

The uniformity of size of the European and Asia Minor specimens is noteworthy, as is the transitional character of the Indian population (between those of central Asia and Caucase—Persia) and the North African population (between those of Europe and the others in Africa and Arabia) and the signifi-
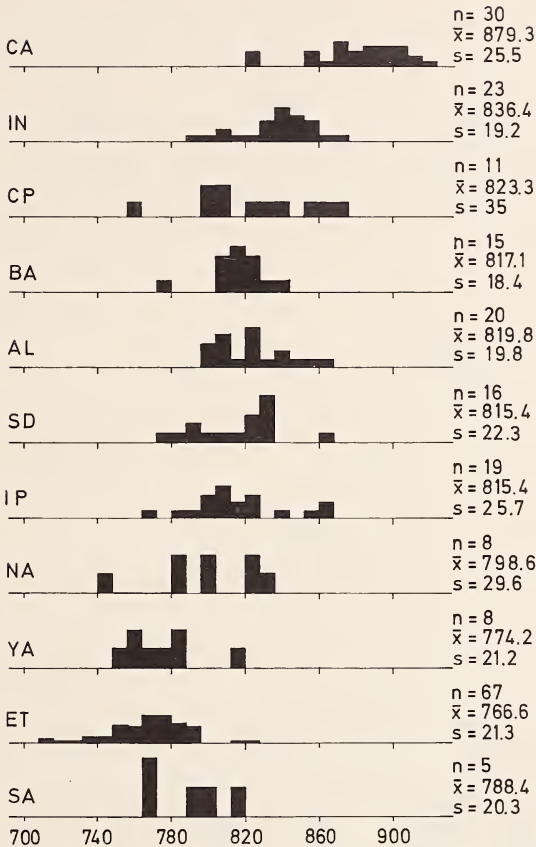
Table 4: "t"test matrix for the average length of the wing. We refer to the populations as in Fig. 3. ( ) = sample size; +++ = p<0.001, ++ = p <0.01, + = p<0.05.

	CA (30)	IN (23)	CP (11)	BA (15)	AL (20)	SD (16)	PI (19)	NA (8)	YA (8)	ET (67)	SA (5)
CA	—										
IN	+++ 6.987	—									
CP	+++ 4.859	1.164	—								
BA	+++ 9.358	++ 3.112	.535	—							
AL	+++ 9.262	++ 2.776	.299	.428	—						
SD	+++ 8.802	++ 3.057	.656	.223	.620	—					
PI	+++ 8.513	++ 2.952	.657	.225	.608	.009	—				
NA	+++ 7.046	++ 3.372	1.657	1.604	1.868	1.418	1.394	—			
YA	+++ 11.920	+++ 7.322	+ 3.787	+++ 4.830	+++ 5.246	+++ 4.416	+++ 4.316	1.895	—		
ET	+++ 21.119	+++ 14.613	++ 5.211	+++ 9.316	+++ 10.379	+++ 7.822	+++ 7.567	++ 2.970	.965	—	
SA	+++ 8.926	+++ 4.846	+ 2.506	+ 2.802	++ 3.120	+ 2.543	+ 2.495	.739	1.204	+ 2.312	—

Fig. 5: Frequency of different wing lengths in each population. N: size of the sample, x̄: average, s = standard deviation.

cantly larger size of the South African specimens compared to those of Ethiopia.

The gradation of variation and its direction suggest a latitudinal and/or climatic association. We have correlated the average wing length in each population with the average latitude of its area of distribution and with different climatic variables of this, and at the same time we relate these with each other (r_s, Spearman's rank correlation coefficient is used). The results appear in Table 5.

There is a strong negative correlation between wing length and minimum temperatures (average of the coldest month and absolute minimum average) and annual average temperature, and a moderate positive correlation between wing length and latitude. Granted that the four geo-climatic variables are in turn correlated significantly among themselves (which supposes a certain redundance in
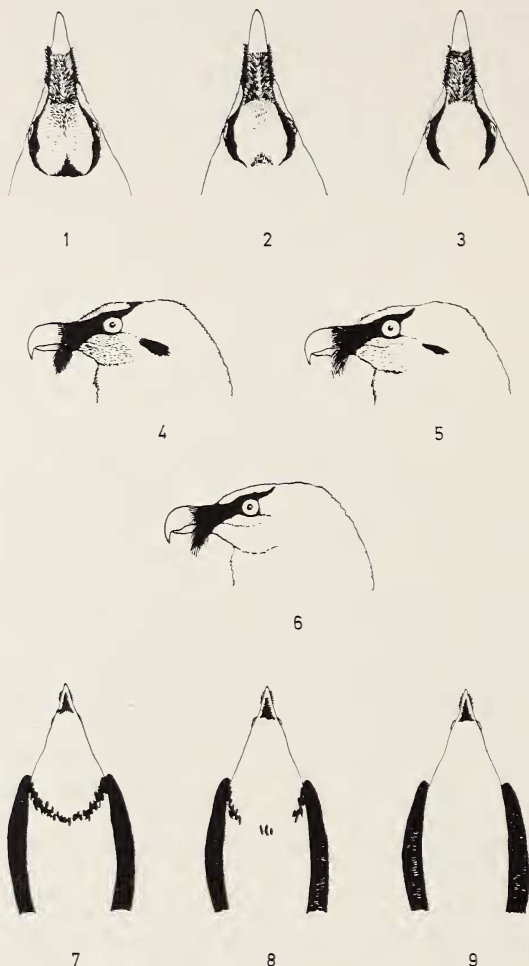
Fig. 6: Plumage patterns of adult Bearded Vultures used as characters for the study of the geographic variation. 1: Crown black and white, 2: crown dirty white, 3: crown completely white, 4: well developed ear tuft and numerous black filoplumes on the chin, 5: intermediate ear tuft and few black filoplumes on the chin, 6: absence of ear tuft and black filoplumes on the chin, 7: complete or almost complete pectoral band, 8: traces of pectoral band, 9: absence of pectoral band.

the previous results) and considering that the significant relation between average annual temperature and average of the absolute maximum temperature does not show as an influence of the latter on wing length, we are inclined to believe

in the existence of a relationship of dependance between low temperatures and increase in size, according to Bergmann's rule.

T a b l e 5: Correlation matrix of the average length of wing and some climatic variables. W = wing length; L = latitude; T = average annual temperature; M = average temperature of the warmest month; m = average temperature of the coldest month; Ma = average annual absolute maximum temperature; ma = average annual absolute minimum Temperature; P = average annual precipitation.

	W	L	T	M	m	Ma	ma	P
W	1	+ .598	+++ —.866	—.266	+++ —.934	—.503	++ —.842	.009
L		1	+ —.682	—.318	++ —.736	—.336	+ —.748	—.216
T			1	.527	+++ .954	+ .712	+++ .876	.039
M				1	.409	+ .742	.112	—.239
m					1	.524	+++ .948	.048
Ma						1	.418	—.191
ma							1	.291
P								1

Geographical variation in plumage patterns

Crown (Fig. 6: 1, 2 and 3): We distinguished 3 states with regard to this feature: 1. — Back part of the crown completely white (Ww). 2. — Same area dirty white or slightly marked with black (W). 3. — Same area clearly black and white (BW).

The individuals from central Asia, India, Caucase—Persia, Balkans, Sardinia and Yemen are mostly black and white (BW) with regard to this character. Many of the specimens of the Alps are dirty white (W) which is the predominant state in the Iberian Peninsula and North Africa. The most frequent state in Ethiopia and South Africa is pure white (Ww) (Table 6). The transition that the populations of Iberia and North Africa represent between those of Eurasia and Eastern and South Africa ist therefore noteworthy. Also, the similarity between the adult specimens from the Yemen and the remaining specimens from Eurasia ist noticeable, all of these being clearly different from the Ethiopian specimens. This has already been mentioned by Bates (1939).

Table 6: Number of individuals with every pattern of design in each population. Crown: Ww = White, W = Dirty white, BW = Black and white. Ear tuft: 1 = Well developed, 2 = Little developed, 3 = Absent. Pectoral band: 1 = Complete, 2 = Intermediate, 3 = Absent. Breast and belly: 1 = Whitish, 2 = Reddish.

	Crown			Ear's tuft			Pectoral band			Breast & belly	
	Wa	W	BW	1	2	3	1	2	3	1	2
Central Asia	0	2	16	16	2	0	17	0	0	15	3
India	0	0	9	5	4	0	9	1	0	3	6
Caucase−Persia	0	0	5	4	1	0	3	2	0	4	1
Balkans	0	1	5	6	0	0	5	2	0	3	3
Alps	0	3	6	8	1	0	7	0	1	9	0
Sardinia	0	0	6	6	0	0	6	0	0	6	0
Iberia	0	4	2	3	3	0	2	5	0	3	3
North Africa	0	3	3	3	3	0	3	3	1	2	4
Yemen	0	0	2	1	1	0	2	0	0	0	2
Ethiopia	19	8	3	0	0	30	6	15	10	1	29
South Africa	3	1	0	0	0	4	0	3	0	1	3

Table 7: The number of the black filoplumes existing in an area of 3×3 cm on the chin.
x̄ = average number of filoplumes

	Number of specimes with 0 1—8 9—20 >20 black filoplumes				x̄	Range
Central Asia	0	0	7	5	20.3	15—33
India	1	0	1	8	22.6	0—34
Caucase—Persia	0	0	1	4	23.8	14—29
Balkans	0	0	2	4	16.5	9—26
Alps	0	0	2	5	24.9	18—29
Sardinia	0	0	1	5	25	19—33
Iberia	0	2	1	3	17.3	3—34
North Africa	2	0	2	1	12.2	0—22
Yemen	0	0	2	0	15	11—19
Ethiopia	28	2	0	0	0.1	0—2
South Africa	3	0	0	0	0	0—0

Black filoplumes on the chin (Fig. 6: 4, 5 and 6): As an estimation of the relative density of these filoplumes, we have counted the number of them in a 30 x 30 mm area on each individual chin. The results, grouped into populations, are shown in Table 7.

All the specimens from Eurasia except one (from India) show black filoplumes in the throat and, with the exception of two (from Iberia), there were always nine or more filoplumes in the area considered. Of the five specimens from North Africa, however, two lack these filoplumes, as is the case with practically all those of Ethiopia and South Africa. Again, the populations of Iberia and North Africa are forms of transition between those of Eurasia and Eastern and South Africa and the specimens from the Yemen are closer to the Eurasian than to the African.

Black tuft in the ear: We distinguished three states: 1. — Well developed tuft (Fig. 6: 4). 2. — Visible but little-developed tuft (Fig. 6: 5). 3. — No tuft (Fig. 6: 6).

The black tuft is missing in the Ethiopian and South African specimens, whereas it is always present in more or less developed state in all the others (Table 6). We must also point out that in spite of the small sample size, only the populations of the Balkans and Sardinia are totally homogeneous, all their specimens being included in a single category.

Pectoral band: We distinguished three states: 1. — Complete or almost complete pectoral band (Fig. 6: 7). 2. — Traces of pectoral band which do not amount to half of the potential length (Fig. 6: 8). 3. — No pectoral band (Fig. 6: 9). The distribution of the specimens into one or another category is shown in Table 6.

With the exception of Iberia, all the remaining Eurasian populations (including Yemen) have a greater number of specimens of type 1 than of both types 2+3 altogether. In Iberia and North Africa there is a tendency of the pectoral band to disappear, this being a striking feature in Ethiopia where only 19 % of the specimens are of type 1, while 32 % are of type 3.

Reddish color on throat, breast and belly: Although only individuals in captivity have really white lower parts, we can distinguish, among those collected in the wild, those with more or less reddish parts from those which are of a dirty white or creamy color. On this basis we have divided the specimens into two categories: 1. — With white lower parts. 2. — With reddish lower parts. The distribution of the individuals of the different populations into these categories is shown in Table 6.

In almost all the populations there are as many white individuals as red ones. Only those from restricted areas like Sardinia and the Alps, or from those where little material exists as in the Yemen, are homogeneous in this respect. In any case, this feature has little validity for the study of the geographic variation on a large scale, since Berthold (1967a, 1967b, etc) despite the vigorous opposition from Clancey (1968a, 1968b, etc), has demonstrated that the reddish tones come from iron oxide sticking to the feathers and so it can vary between closed localities according to the nature of the ground, meteorology, etc.

Geographical variation in other characters

Some characters which vary geographically are too subtle or require the use of sophisticated methods to be able to be given a quantitative estimate with reasonable objectivity. Such is the case with the tonality of the back and the feathering on the legs.

Tonality of the back. The back feathers of the Bearded Vulture are dark on the edges and a little lighter in the center, with a white or creamy rachis stretched over the apex and strongly contrasting with the rest. The width of the light central strip, the darkness of the edges and the whiteness of the rachis vary from population to population. The lightest individuals are found in central Asia and the darkest in Ethiopia and South Africa. In the first case the rachis is absolutely white, while in Ethiopia it is generally tinted a reddish color, the same as the feathers of the lower parts.

Feathering on the legs. The Eurasian specimens have a thicker, denser plumage than the African, a characteristic which is particularly evident on the legs. All the specimens from central Asia have thick plumage in the legs as far as the base of the toes, whereas on those from Ethiopia and South Africa the feathers of the distal parts of the legs were almost always missing.

Discussion

As for age variation, it must be considered that replacement of feathers requires, in the case of vultures, a great energetic expense. Therefore, the molting process may be considerably influenced by the availability of food. Correspondence among absolute ages and plumage phases shown in Table 3 must therefore be considered a mere approximation to reality.

All the morphological characteristics of *Gypaetus barbatus* considered in this study show gradual geographic variation, if we exclude the reddish color of the lower parts which varies in an irregular manner. In any case the extremes of variation are found in Asia and Ethiopia, the transition being established through North Africa and the Iberian Peninsula and not through Arabia and the Middle East. It is in size only that the Arabian specimens are like the Ethiopian, while all of these are similar to those of South Africa though a little smaller.

The negative correlation between the size of the animal and the annual average of minimum temperatures suggests a bioenergetic motivation according to the modern interpretation of the Bergmann's ecogeographical rule (Mayr, 1963, 1976, Kendeigh, 1969, James 1970). Various authors have offered evidence or arguments on the influence of other factors on the body size of homeothermic animals. Among these factors we could quote interspecific competition (Rosenzweig, 1966, Schoener, 1969, McNab, 1971, MacArthur, 1972, Cody, 1974), the size of the available food (Valverde, 1967, Schoener, 1969, McNab, 1971), the primary productivity as an estimation of the quantity of food available (Rosenzweig, 1968), etc. However these factors must have only a slight influence on the determination of body size of the Bearded Vulture, as it is practically lacking in competitors (Houston, 1973, König, 1976, Hiraldo, 1977), it eats carrion and live animals of very varied size (from small mammals and birds to large carcasses: Cano & Valverede, 1959, Terrasse & Terrasse, 1974, Dementiev & Gladkov, 1966, Newmann, 1969) and the clinal variation of its size does not correspond to gradual change of the food available. Consequently the application of Bergmann's rule to *Gypaetus barbatus* can be interpreted not only as an empirical fact, but also in the classical way, as the result of a selective pressure in favor of an optimal surface to volume ratio.

To determine the adaptive value of the variation in pattern and coloring is much more difficult, specially considering that none of the quantitative estimations is correlated significantly with the different geo-climatic variables (r_S Spearman rank correlation coefficient). The differences of pattern between the specimens from the Yemen and Ethiopia, despite the geographic and climatic proximity of both regions, and the similarity between those of Yemen and the remaining from Eurasia, gives rise to considering a fairly stable genetic base for the characters considered. This would also explain the homogeneity of the Sardinia population, which most likely originates from a few invaders (founder

effect) and its relative dissimilitude with the Iberian and North African populations, although they are geographically close and the climate is similar.

On the other hand, details of coloring or pattern norms apparently "neutral", as it is the case of some of the characters above discussed, can be simply incidental subproducts of genes which are kept in the gene pool to give rise to other physiological advantages (Mayr, 1963), being these unknown for us.

As for the characteristics which have not been quantitatively estimated, it seems to be logical to relate the density of the plumage with the temperature, since the individuals with less plumage on the leg are found in Africa. The lighter tonality of the central Asia specimens (cold, dry climate) and the darker tonality of the African (warm climate) could perhaps be considered in the light of the debated and not well-explained rule of Gloger (Mayr, 1963).

If as we presumed the Bearded Vultures of Arabia are genetically closer to the Asian than to the African, we are forced to deduce that either size is a very plastic characteristic, or the selective pressure of the temperature on size is much stronger than the pressure suffered by the remanining characteristics studied. Recent and diverse studies effectively show the great influence of non-genetic factors on size and body proportions, i.e. the experiments of Weaver & Ingram (1969) with pigs from the same litter but raised at different temperatures, whose phenotypes respond to the rules of Bergmann and Allen. Selander (1971) quotes in the same manner various cases of variation in wing length of some birds motivated by climatic or trophic factors.

Acknowledgments

Summary

Biometry and plumage variation of 252 study skins of Bearded Vulture are analysed. Young specimens are dark and require two moultings before they acquire an imperfect adult plumage, which happens at the age of about 5 years. The intermediate, immature plumage is similar to that of the young, from which it basically differs in the type of back feathers, the appearance of brown semiplumes on the head and an increase of steel grey tones on the flight feathers. An approximate correspondence among absolute ages and plumage phases is shown in table 3. Geographical variation is noticeable. Size differs clinally, following Bergmann's eco-geographical law. The largest specimens are those of Central Asia and the smallest those of Ethiopia. As far as plumage is concerned, the neatest patterns are to be found in Southern and Eastern Africa, while in Asia blurring in the patterns is more common. The transition between these two extremes is to be found

in the Iberian Peninsula and Northern Africa, and not in the Yemen, as might be expected.

Zusammenfassung

Biometrie und Gefiederunterschiedlichkeiten des Lämmergeiers werden untersucht. Die Untersuchungen wurden an 252 Exemplaren aus verschiedenen Museumssammlungen durchgeführt. Juvenile Lämmergeier sind dunkel und wechseln das Gefieder zweimal, bevor sie ein noch unvollkommenes adultes Gefieder erreichen, was im allgemeinen im 5. Lebensjahr stattfindet. Das unfertige Zwischengefieder ist dem des juvenilen Geiers ähnlich, von dem es sich hauptsächlich durch die Art der Rückenfedern, das Erscheinen von braunen flaumartigen Federn auf dem Kopf und Verstärkung des stahlgrauen Tones der Federn auf den Schwingen unterscheidet. In Tabelle 3 wird das ungefähre Verhältnis zwischen absolutem Alter und Gefiederphasen dargestellt. Die geographischen Unterschiede sind beachtenswert. Die Größe schwankt klinal und folgt dem ökogeographischen Gesetz Bergmanns. Die größten Exemplare kommen in Zentralasien, die kleinsten in Äthiopien vor. Am deutlichsten ist die Zeichnung bei den Lämmergeiern aus Äthiopien und Südafrika, am undeutlichsten bei denjenigen aus Asien. Der Übergang zwischen diesen beiden Extremen findet auf der Iberischen Halbinsel und in Nordafrika statt und nicht, wie angenommen werden könnte, in Yemen.

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